Olfactory and Visual Stimuli Affecting Host Plant Detection in *Homalodisca coagulata* (Hemiptera: Cicadellidae)

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ABSTRACT The relative effects of visual and olfactory stimuli on host plant detection in immature and adult *Homalodisca coagulata* Say (Homoptera: Cicadellidae) were studied using a novel olfactometer and factorial experimental designs. Colored, gray, and white cards were used as visual targets. Each card was attached to a glass thistle tube from which host-plant odor (from *Vigna unguiculata* L.) or blank, humidified air was dispensed. Visual + odor stimuli combinations were presented in no-choice tests. Nymphs were released onto a perch stick downwind from the target. Nymph response to color + odor treatments was measured by the duration of orientation behavior, residence time on the perch, and percentage of individuals that jumped to the target. The assay was modified so that adults crawled from the perch onto the target. Adult response was measured by the duration of individual behaviors (e.g., foraging) and by their position and residence time on the target. Both main effects and interactive effects of the stimuli were observed. Nymphs showed a decrease in orientation and residence times in the colored target + host odor treatments and increased jumping response in the gray + host odor treatment. When adults were exposed to host odor, the duration of foraging behavior increased, whereas crawling and phototactic behaviors decreased. Although nymphs and adults responded to visual stimuli + blank air treatments, host odor enhanced their responses. The primary effect of host odor on host detection behavior may be to enhance *H. coagulata* responsiveness to visual cues.

KEY WORDS glassy-winged sharpshooter, olfactometer, chemoreception, color perception, host-finding behavior

The glassy-winged sharpshooter, *Homalodisca coagulata* Say (Homoptera: Cicadellidae), is a primary vector of *Xylella fastidiosa*, a bacterium that causes scorching diseases in a number of major crop plants (Mizell and French 1987, Blua et al. 1999, Redak et al. 2004). It is polyphagous and obtains all of its nutrients from xylem fluid (Brodbeck et al. 1999, Redak et al. 2004). Because internal water stress and nutrients levels in xylem can fluctuate rapidly, individuals must effectively track the physiological state of their host plants to obtain adequate nutrients (Mizell and French, 1987, Andersen et al. 1992, Brodbeck et al. 1999, Redak et al. 2004, Tipping et al. 2004). Indeed, the distribution patterns observed in *H. coagulata* populations are spatially and temporally complex and may reflect the occurrence and distribution of hosts with suitable xylem tension and nutrient levels (Brodbeck et al. 1999, Mizell and Andersen 2003, Daane and Johnson 2003, Groves and Chen 2004, Redak et al. 2004, Groves et al. 2005, R. Groves, personal communication).

While its attraction to bright yellow is well known (Hix et al. 2003, Tipping et al. 2004), a stimulatory effect of host plant chemicals on *H. coagulata* host-finding behavior has not been shown with certainty (Leal 2001, Leal et al. 2001, Mizell 2001, Mizell and Andersen 2001). However, visual stimuli alone may not provide enough information for *H. coagulata* to efficiently track its host plants, especially those whose physiological suitability can vary on a daily basis (Prokopy and Owens 1983, Harris and Foster 1995, Raguso and Willis 2002). Host volatiles have a stimulatory effect on host-finding behavior in other cicadellids (Saxena and Saxena 1974, Todd et al. 1990b), and given the vagility of *H. coagulata*, it is to be expected that chemical stimuli play some role in detecting and locating host plants.

In this study, we examined the behavioral responses of immature and adult *H. coagulata* to host plant odor and humidified, blank air when presented with colored and achromatic visual stimuli. A novel olfactometer and accompanying assays were developed to observe and quantify behavioral responses to combinations of visual and olfactory stimuli (Fig. 1). The methods were tai-

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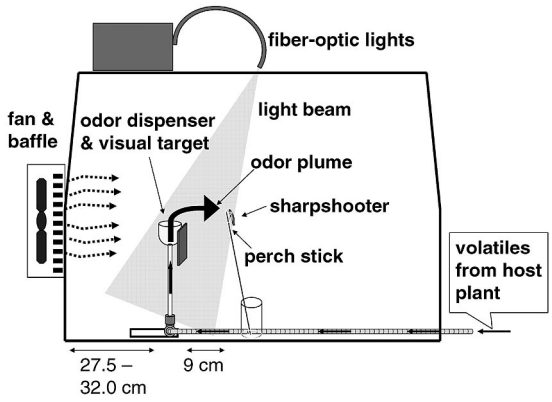

Fig. 1. Diagrammatic representations of an olfactometer designed to measure the responses of adult and immature *H. coagulata* to combinations of visual and olfactory stimuli.

lored to several behavioral aspects of *H. coagulata;* e.g., a tendency to remain on stems, explore substrates with their mouthparts, and display a distinctive scanning behavior before jumping or flying. Responses were measured with no-choice tests in which a single color–odor combination was presented to individuals perched on a release stick. The results are discussed in terms of the relative effects of visual and olfactory stimuli on different aspects of *H. coagulata* host detection behavior.

Materials and Methods

Insects and Plants. A colony of *H. coagulata,* established from locally local populations and maintained at the USDA Subtropical Agricultural Research Center in Weslaco, TX, provided study insects. Field-caught individuals were periodically introduced into the colony to maintain genetic heterogeneity. The colony was reared primarily on cowpea, *Vigna unguiculata* L, in a greenhouse at 27–35°C and a 16:8 (L:D)-h photoperiod. Cowpea plants were grown from seed under the same greenhouse conditions as described above.

Bioassays. The olfactometer chamber was made from a clear polymer box (85 by 59 by 49 cm; Fig. 1). A computer cooling fan (20 W, 10.5 cm diameter, model 273–241C; Radio Shack, Ft. Worth, TX), connected to a voltage regulator, generated airflow (≈10.5 ± 0.25 m/min) across the chamber. A plastic baffle covered with organdy fabric was placed next to the fan to create laminar airflow. Airflow rate was determined with an air velocity meter (model 8340; TSI, St. Paul, MN). Experiments were conducted in a ventilated room at 27–28°C and 35–40% RH between 0800 and 1200 hours.

Air for the odor delivery systems came from a pressurized cylinder containing ultra-purified air and was regulated at a rate of 1.3 liters/min (air delivery system model ADS-4AFM4 C.4; Analytical Research Systems, Gainesville, FL). Air from the pressurized cylinder was bubbled through 200 ml of deionized water to humidify it. Cowpea was selected as the source of host plant odor because it was used to rear the *H. coagulata* used in theses studies. Host plant odor for the tests was provided by four cowpea sprigs placed inside a glass-volatile collection vessel (4 liters; Analytical Research Systems). The sprigs were cut from 7- to 14-d-old plants, inserted into capped florist tubes (Floral Suppliers Syndicate, Camarillo, CA) filled with 10-5-14 (N-P-K) hydroponic solution (MaxiGro; General Hydroponics, Sebestopol, CA), and placed into the volatile collection vessel 30 min before testing. The vessel was illuminated with two horticultural spotlights (50 W). The sprigs were periodically checked to ensure that they remained turgid and suitable as an odor source during the assays. Humidified air (blank air) circulated through an empty volatile collection vessel was used to as a control for possible stimulation from transpiration vapor (R. Groves, personal communication).

Because no-choice tests were used in the behavioral assays (see below), test insects were exposed to either host odor or blank air during a particular test. Separate air lines were used to carry host odor and blank air into the olfactometer. The air lines terminated in separate Swagelok T-shaped connectors (6.25 mm i.d.) mounted to the olfactometer floor. Host odor and blank air were dispensed into the olfactometer through the aperture of a glass thistle tube (4.0-mm stem i.d.; 42.0-mm aperture diameter) inserted into the appropriate T-connector (Figs. 1 and 4). To avoid contamination, separate thistle tubes were used for each treatment. Examination with dry ice vapor showed that the dimensions of the odor plumes dispensed at each of the two T-connector positions were similar. At the completion of each day's testing, the odorant system was dismantled and cleaned. *H. coagulata* used for the experiments were returned to the colony immediately after completion of testing. Most were tested once, but occasionally insects would be reused as test subjects after 5–7 d elapsed between tests.

Tests of Immatures. Paint sample cards (7.5 by 7.5 cm; BEHR Process, Santa Ana, CA) were used as visual targets. The cards were affixed to the thistle tube, which permitted presentation of specific color–odor combinations to the nymphs (Fig. 1). The spectral qualities of the paint sample cards were verified by measuring their reflectance spectra in the 350- to 700-nm range with a hand-held spectroradiometer (FieldSpec HandHeld; Analytical Spectral Devices, Boulder, CO) under illumination conditions used for the assays (described below; Fig. 2). Because of its attractiveness to *H. coagulata* nymphs (Tipping et al. 2004), bright yellow was selected to serve as a positive control for visual attraction. The yellow card (BEHR 'Citrus Splash' S-G-370) had a bright yellow appearance and sigmoidal reflectance curve asymptotic at ≈570 nm. Nymphs frequent the growing shoots of their host plants, and a bright green card was chosen because of its resemblance to new foliage. The green card (BEHR 'Citrus Crush' S-G-410) had a maximal reflectance peak at 540 nm and bright lime-green appearance. White and gray cards were selected as

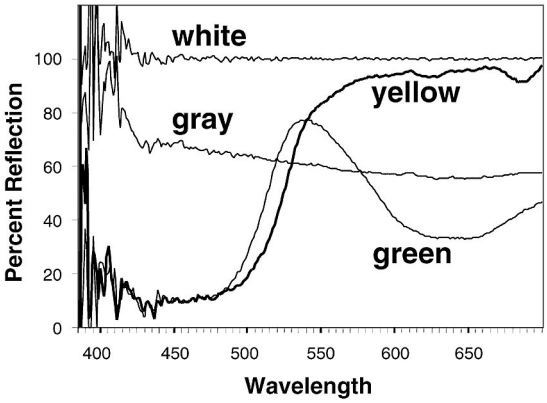

Fig. 2. Spectral reflectance of paint sample cards used for visual targets in behavioral assays.

achromatic visual targets with different reflectance intensities. A sample card (BEHR 'White' W-F-620) with a "pure white" appearance and a high level of uniform reflectance intensity was selected as the white target. A card (BEHR 'Skyline Steel' 750E-3) with a light gray appearance, uniform reflectance, and midscale reflectance intensity was selected to provide a moderate degree of contrast to the white target.

The visual target and thistle tube (hereafter referred to simply as "target") were illuminated with two fiber optic lamps (model 180; Dolan-Jenner Industries, Boxborough, MA, and model NI-150; Nikon Instruments, Melville, NY). The illumination level of the target, measured with a light meter (model 401025; Extech Instrument, Waltham, MA), was ≈1675 Lux. The interior of the olfactometer was covered with matted black paper to dampen light reflections.

To enhance response levels, nymphs were starved overnight. Fifty third- and fourth-instar nymphs were collected between 1700 and 1800 hours the evening before testing and placed individually into plastic vials (6.8 cm high and 2.5 cm diameter) with moistened filter paper strips and perforated caps. The nymphs were held in an incubator at 25 ± 2°C with a 16:8 (L:D)-h photocycle that was synchronized with the colony photocycle. During testing, the vials were placed adjacent to the olfactometer and illuminated with a 15-W fluorescent lamp.

For each test, an active nymph was selected and transferred into the olfactometer. Once the vial was positioned downwind from the target, an artist's paintbrush was inserted into the vial and positioned so that it leaned toward the target (Fig. 1). The dimensions of the paintbrushes (shaft, 5.0 mm diameter by 171 mm length) were similar to those of a cowpea plant used for rearing. In this respect, the paintbrush mimicked the host's stem and provided a substrate on which nymphs could behave normally while in the olfactometer. The tip of the paintbrush was positioned 9.0 cm from the thistle tube rim and 5 mm above the thistle-tube aperture (Fig. 1). A visible stream of dry ice vapor exhausted from the thistle tube indicated that the odor plume flowed across the top 2.5 cm of the paintbrush (hereafter referred to as the "perch"). The spatial arrangement of perch and target afforded efficient presentation of only a single odor to the insect, thus only no-choice tests with a single odor were used in these studies. A cleaned perch was used for each test. This reduced the likelihood that chemicals from the odor plume would become deposited on the perch, in which case behavioral responses attributed to olfaction would be caused by contact detection or a combination of both contact and olfactory detection.

Three behavioral parameters were used to evaluate nymph response to the stimuli treatments (Fig. 3A). Residence time was the amount of time that a nymph remained on the perch. It began when the nymph crawled above the vial and ended when the nymph either jumped off or remained on the perch for 600 s or more. Orientation time was the amount of time a nymph displayed a "stereotypical" orientation behavior (Figs. 3A and 4A). Target choice was scored according to whether the nymph jumped to the target, other part of the olfactometer, or remained on perch stick. Comparison of the values of these three behavioral parameters among the different treatments permitted determination of the relative stimulatory effects of color, odor, and color + odor combinations. Residence- and orientation time data were compiled only for nymphs that jumped to the target. Nymphs that remained in the vial longer than 180 s, did not jump from the perch stick after 200 s of continuously orientating, or did not display orientation within 600 s of crawling onto the perch were excluded from further analysis.

In the initial experiment, nymph response to a foliar color, lime green, and a supra-stimulatory color, bright yellow (Prokopy and Owens 1983), was tested with the following 2 by 2 factorial design: bright yellow + blank air; bright yellow + cowpea odor; lime green + blank air; lime green + cowpea odor. At least 30 nymphs were tested for each treatment. Because

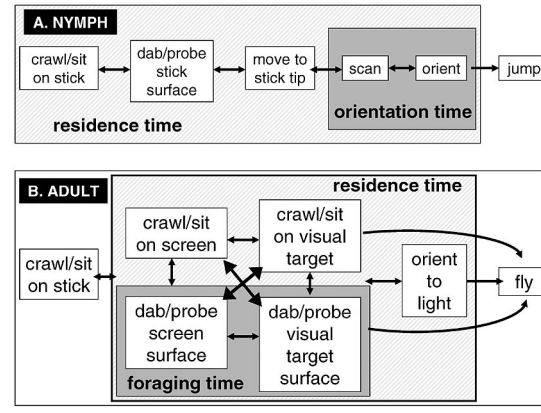

Fig. 3. Diagrammatic depiction showing a representative sequence of behaviors displayed during assays and the temporal relationships of the individual behavioral parameters used to measure response to test stimuli. Arrows represent transitions from one behavior to another. (A) Nymphs. (B) Adults.

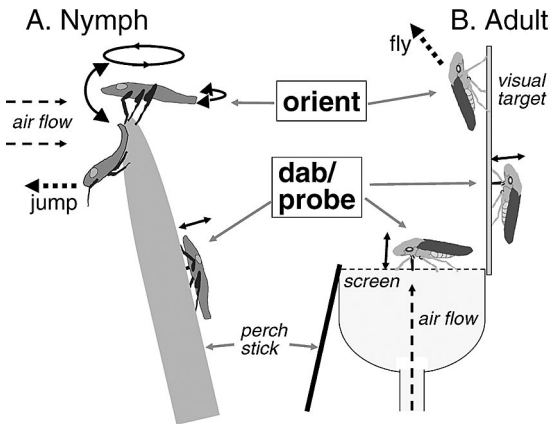

Fig. 4. Diagrammatic representations of stereotypical behaviors displayed by *H. coagulata* during behavioral assays. Solid black arrows indicate movement direction(s) made during each particular behavior. (A) Nymphs. (B) Adults.

nymphs are attracted to colors that simulate foliage, such as bright yellow (Tipping et al. 2004), a high level of response was expected, even without stimulation from host odor. However, an increase in orientation response in the presence of host odor would indicate that the host odor had a stimulatory affect.

In the second experiment, response to achromatic visual stimuli, gray and white, was measured. Because Tipping et al. (2004) observed a negligible response of *H. coagulata* nymphs to gray and black targets, a low response to gray and white targets was expected in this experiment. Again, if nymphs were stimulated by host odor, their response to achromatic targets would be expected to increase. A bright yellow treatment was included as a check to ensure that the nymphs were responsive to visual cues and to provide a comparison of the relative stimulatory effects of achromatic versus colored stimuli. The following 2 by 3 factorial design was used: white + blank air; white + cowpea odor; gray + blank air; gray + cowpea odor; bright yellow + blank air; and bright yellow + cowpea odor. Thirty nymphs were tested for each of the four achromatic treatments, whereas 15 nymphs were tested for the two color treatments.

Tests of Adults. The relative stimulatory effects of visual + olfactory cue combinations in adult *H. coagulata* were tested with the following 2 by 2 factorial design: bright yellow + blank air; bright yellow + host odor; white + blank air; white + host odor. Because bright yellow is very attractive to adult *H. coagulata* (Hix et al. 2003), adult response to the different treatments was expected to be similar to that obtained with the nymphs.

During preliminary tests, adults invariably flew upward from the perch to the light rather than horizontally to the target. Therefore, the perch-target arrangement was modified into a single platform (Fig. 4B), and retention (arrestment) time on the platform and foraging behavior were used as the primary parameters to evaluate their responses. The platform was comprised of a visual target attached to an odor dispenser (Fig. 4B). The visual target was an obelisk (62 mm height by 20 mm width) cut from a paint sample card. The perch was positioned against the thistle tube so that adults crawled directly onto an organdy screen placed over the aperture. Adults were exposed to both visual and olfactory stimuli when they were located on the tip of the perch, screen, and leeward side of the visual target. All other experimental conditions were the same as those used for the nymphs.

At the start of each test, the perch was inserted into the holding vial (3.1 cm diameter by 6.0 cm height). Data collection started when the adult crawled onto the screen and terminated when it either flew from the platform or continuously oriented to the light for 30 s. During each test, adults were scored as being engaged in the following behaviors: sitting (=remaining stationary with the mouthparts not extended), crawling, grooming, phototaxis (=orienting to the olfactometer light), and foraging (Figs. 3B and 4B). The duration of each behavior and the location where it took place was recorded.

Foraging comprised two behaviors (Backus 1985, Almeida and Backus 2004), which were recorded separately. Labial dabbing is a generalized response shown when leafhoppers initially come into contact with plant surfaces. It is characterized by the labium held at a right angle to the body axis while the proboscis is repeatedly extended and retracted. Probing is characterized by the sharpshooter appressing the tip of its labium to the substrate while it remains more or less stationary. During probing, the stylet can penetrate hard substrates, such as wood (Backus 2000).

Compilation of these measurements by treatment permitted the following calculations to be made for each observation: (1) total time on the screen and visual target (=residence time), (2) percentage of residence time engaged in foraging behavior, (3) percentage of foraging time spent specifically on the screen, (4) percentage of foraging time spent specifically on the visual target, and (5) percentage of time spent engaged in other behaviors (e.g., grooming, phototaxis).

Inactive or nonresponsive individuals were omitted from the analysis. This included adults that remained in the vial (>120 s), on the perch stick (>600 s), or which flew after only a brief (<20 s) contact with the target. Infrequent and brief intervals when the adults crawled onto the side of the thistle tube were deleted from the data sequence because discernment of their behavior was not always possible at this location; e.g., discernment of probing versus sitting. For each treatment, data were collected from at least 30 active adults.

Analysis. Before analysis, continuous data were log-transformed and proportional data were arcsine-transformed to stabilize their variances (Zar 1999). The effects of color, odor, and color + odor interactions were determined by two-way analysis of variance (ANOVA) by the Proc GLM of SAS (SAS Institute 1999) on orientation and residence times for nymphs and residence time, percentages of time spent forag-

ing, on the screen or on the visual target, and percentage of time spent engaged in other behaviors for adults. Where significant, *F*-values were obtained, treatment means were separated using the Student-Newman-Keuls multiple range test (Zar 1999). The percentage of nymphs selecting different visual target–odor background combinations was compared by a log-likelihood test (*G*-test) of 2 by 3 or 2 by 2 contingency tables (Zar 1999).

Results

The majority of *H. coagulata* conditioned overnight and tested in the olfactometer were active and responded positively. Approximately 65 and 58% of, respectively, nymphs and adults tested were responsive and included in the analysis.

Orientation and Foraging Behavior. Both adults and nymphs displayed dabbing and probing behavior (Figs. 3 and 4). While orienting toward the target or light source, the nymphs displayed a stereotypical scanning behavior in which they faced toward the stimulus while moving back and forth laterally (Fig. 4A). During scanning, nymphs frequently changed their vertical and horizontal angle of orientation. The intensity and duration of the scanning behavior varied among individual nymphs. Nymphs arched their bodies before jumping (Fig. 4A), and their subsequent jumping motions were strong and directed. Before flying toward the light, some adults displayed a scanning behavior similar to that of the nymphs (Fig. 4B).

Nymphs. Because there was no difference in the percentages of nymphs that jumped to the bright yellow (73%) versus the lime green (71%) targets, data on residence and orientation times were pooled, and the following treatments analyzed: colored target + host odor and colored target + blank air. Nymphs exposed to host odor had significantly shorter residence ($F = 4.26$; df = 1,123; $P = 0.041$) and orientation times ($F = 8.39$; df = 1,123; $P = 0.005$) compared with nymphs exposed to blank air (Fig. 5).

Relative to the gray and white targets, mean orientation and retention times were approximately threefold lower when the nymphs were presented with the yellow target, irrespective of odor treatment (Fig. 6). The effects of odor and odor + color interaction were nonsignificant for orientation and residence times. Only color significantly affected both residence time ($F = 12.82$; df = 2,98; $P = 0.001$) and orientation time ($F = 25.42$; df = 2,98; $P = 0.001$). However, for clarity, mean values are presented for all visual target-odor treatment combinations (Fig. 6).

While no differences were seen in the residence and orientation times in the gray target treatments (Fig. 6), the percentage of nymphs that jumped to the target in the gray + host odor treatment was twice as great as the percentage of nymphs that did so in the gray + blank air treatment (Fig. 7). The percentage of nymphs that jumped to the targets did not vary between odor treatments when presented with the yellow or white targets (Fig. 7).

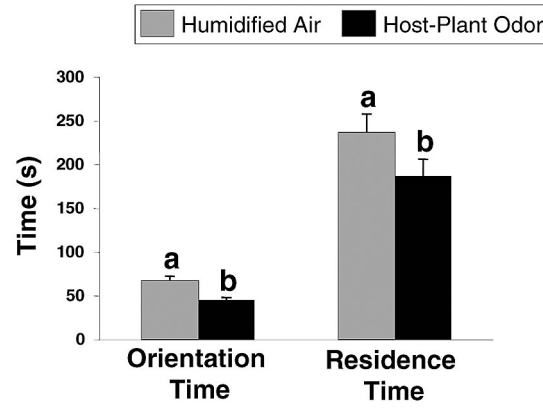

Fig. 5. Responses of *H. coagulata* nymphs to lime green and bright yellow visual targets when presented with different odor backgrounds. Within-group means (±SE) having different letters are significantly different (orientation time, $P \leq 0.005$; residence time, $P \leq 0.05$). $N = 60$ individuals per color–odor combination (lime green and bright yellow color treatment data pooled; general linear model, SAS Institute 2001).

Adults. Residence time was significantly affected by both color ($F = 7.76$; df = 1,119; $P = 0.006$) and host odor ($F = 11.17$; df = 1,119; $P = 0.001$; Table 1). In the host odor treatments, residence time was significantly longer on the yellow target than the white target. However, in the blank air treatments, residence times on the yellow and white targets were not different. In the yellow treatments, residence time was signifi-

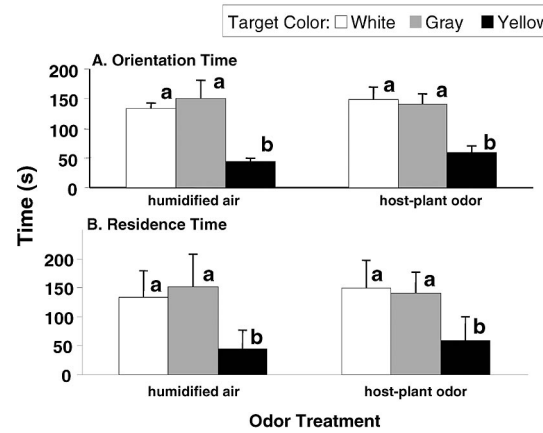

Fig. 6. Responses of *H. coagulata* nymphs to white, gray, or bright-yellow visual targets when presented with different odor backgrounds. (A) Mean orientation times and (B) mean residence times. Within-group means (±SE) having the same letter are not significantly different ($P \geq 0.05$; general linear model, SAS Institute 2001). Data are shown only for individuals that jumped to the target. Number of individuals that jumped to the target/number of individuals tested for each treatment is as follows: yellow + host-plant odor, 17/17; yellow + humidified air, 19/19; gray + host plant odor, 20/30; gray + humidified air, 10/30; white + host plant odor, 17/30; white + humidified air, 19/30.

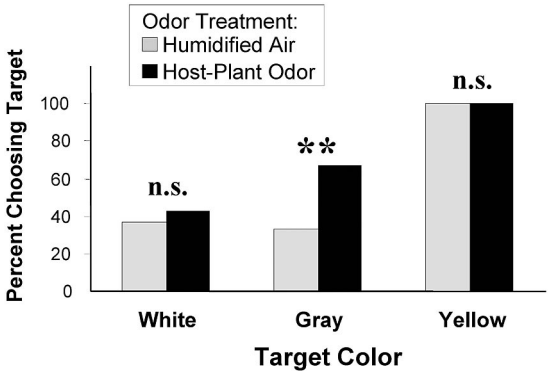

Fig. 7. Percentage of *H. coagulata* nymphs selecting various colored visual targets presented with different odor backgrounds. Columns within the same color treatment group marked with ** are highly significantly different at $P \leq 0.01$ and those marked with n.s. are nonsignificant at $P > 0.05$. $N = 30$ individuals tested per treatment (*G*-test for contingency tables; Zar 1999).

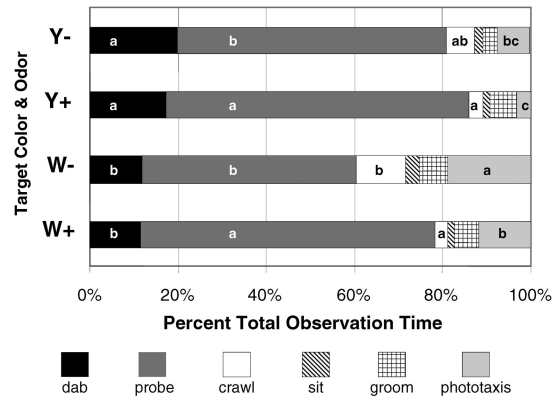

Fig. 8. Time allocation (percent) of individual behaviors of adults. Means within behavior categories marked by asterisks are significantly different at the following levels: labial dabbing, $P < 0.01$; probing, $P < 0.001$; crawling, $P < 0.01$; phototaxis, $P < 0.001$ (color effects) and $P < 0.01$ (odor effects). Y+, yellow visual target plus host plant odor; Y−, yellow visual target plus humid air; W+, white visual target plus host plant odor; W−+, white visual target plus humid air. $N = 30$ adults per treatment.

cantly longer in adults exposed to host odor than in adults exposed to blank air. In the white treatments, there was a trend toward a longer residence time in adults exposed to host odor than exposed to blank air. Foraging behavior was also significantly affected by both target color ($F = 11.25$; df = 1,119; $P = 0.001$) and host odor ($F = 9.42$; df = 1,119; $P = 0.003$; Table 1). The percentage of time spent foraging was greater in the yellow + blank air treatment than in the white + blank air treatment, whereas it was the same on both targets in the host odor treatments. Adults spent more time foraging on the visual target in the yellow + blank air treatment than in the white + blank air treatment. This difference was not observed in the host odor treatments. The percentage of time spent foraging on the screen did not vary among treatments ($F = 0.5$; df = 3,119; $P = 0.68$).

Both main effects and interactive effects of the stimuli were observed with respect to the percentage of time allocated to different behaviors (Fig. 8). Host odor significantly affected the percentage of time spent probing ($F = 11.99$; df = 1,120; $P = 0.001$) and crawling ($F = 6.60$; df = 1,120; $P = 0.01$), whereas labial dabbing was only affected by color ($F = 6.60$; df = 1,120; $P = 0.01$). Phototactic behavior was affected by both color ($F = 19.86$; df = 1,120; $P < 0.001$) and host odor ($F = 6.40$; df = 1,120; $P = 0.013$).

Discussion

The olfactometer permitted us to conduct multifactorial experiments on the effects of visual and chemical stimuli on *H. coagulata* host detection behavior. The same combinations of stimuli were successfully tested on both life stages through rearrangement of the visual target, odor dispenser, and perch stick. Main and interactive effects were observed, showing that *H. coagulata* nymphs and adults responded to both chemical and visual cues from host plants.

An effect of host odor on nymph residence and orientation times was observed in the colored target + host odor treatments. However, because a high percentage of nymphs jumped to the colored targets, chemical stimulus seemed to have no significant effect on their target choice. In the second experiment, host odor did not affect residence and orientation times in

Table 1. Response of *H. coagulata* adults to white or bright yellow visual targets when presented with different odor backgrounds: mean residence time on odor dispenser and visual target; percentage of total residence time spent foraging; percentage of total foraging time spent dabbing or probing screen; percentage of total foraging time spent dabbing or probing visual target

Treatments			Parameters Measured			
Odor	Color	*N*	Residence time (s) ± SE[a]	Total time foraging (%) ± SE	Time foraging on screen (%) ± SE	Time foraging on visual target (%) ± SE
Blank air	White	32	110.3 ± 14.5aA	61.9 ± 4.1aA	25.4 ± 4.7aA	35.8 ± 4.9aA
	Yellow	30	153.7 ± 20.7aA	79.0 ± 3.4bA	20.8 ± 3.6aA	58.2 ± 3.9bA
Cow pea	White	30	173.6 ± 26.5aA	81.3 ± 3.5aB	31.6 ± 7.2aA	48.1 ± 5.9aA
	Yellow	31	241.8 ± 36.9bB	85.9 ± 2.9aA	31.6 ± 5.0aA	54.0 ± 4.7aA

[a] Means followed by the same lowercase letter in each odor group and by the same capital letter in each color group are not significantly different ($P > 0.05$, Student Newman Keuls test).

the gray and white treatments, and their high level of response to yellow was apparently caused entirely by visual stimulus. However, twice as many nymphs jumped to the target in the gray + host odor treatment than in the gray + blank air treatment, a highly significant difference.

These results indicate that certain behavioral parameters should be used to indicate responsiveness to chemical cues only when paired with certain visual stimuli. Nymphs were strongly attracted to green and yellow and jumped to these colors regardless of chemical stimulus. However, even in the presence of these strong visual stimuli, residence and orientation times were influenced by chemical stimuli. Thus, in tests with bright colors, these two behavioral parameters may be more sensitive indicators of nymph response than target choice.

However, target choice may the better indicator of nymph response in tests with neutral or achromatic visual targets. The high percentage that jumped to the target in the gray + host odor treatment showed that they were stimulated by chemical cues when presented with an achromatic visual target. However, achromatic targets may not provide enough visual stimuli to significantly affect residence and orientation time, even in the presence of host odor. The low response to the white target in the presence of host odor supports this idea; i.e., a minimal combination of visual stimuli (e.g., shoot color, reflectance, outline, or shape) may be required to adequately stimulate certain host detection and orientation behaviors (Harris and Foster 1995, Raguso and Willis 2002). Alternatively, it may have been difficult for the nymphs to discern the white target's edge or perceive it as a proximate object.

In adults, residence time and phototactic behavior were influenced by the interaction between chemical and visual cues. Adults had the longest residence time and briefest phototactic displays in the yellow + host odor treatment, whereas phototactic behavior occupied nearly 20% of their time in the white + blank air treatment and mean residence time was only 110 s (Table 1; Fig. 8). Each foraging behavior component was affected by different stimuli. Probing was affected mainly by host odor, whereas labial dabbing was affected mainly by color. Main effects were also observed with respect to the insect's position. Target hue (in this case, yellow) stimulated foraging behavior while the insect was positioned on the visual target but did not have this effect when it was positioned on the screen.

Inputs from various types of visual and olfactory stimuli are likely to be neurologically and behaviorally integrated; i.e., perception of one type of stimulus modifies behavioral response to another type of stimulus (Harris and Foster 1995, Raguso 2001, Raguso and Willis 2002, 2004). Thus, exposure to host odor may have enhanced or synergized the sharpshooters' responsiveness to visual stimuli. This mechanism could explain the decreased residence and orientation timed in the colored target + host odor treatments in the first experiment and the enhanced target selection observed in the gray + host odor treatment in the second experiment. It could also explain the main and interactive effects of the different stimuli on specific adult behaviors; e.g., labial dabbing and probing. Enhanced behavioral response to visual cues after exposure to host odor has been observed in other phytophagous insects. Exposure of *D. maidis* to host plant volatiles increased its response to green light (Todd et al. 1990b). An enhanced response to visual stimuli was observed in immatures and adults of the mirid, *Lygus hesperus*, when they were presented with host plant odor in a Y-tube (Blackmer and Cañas 2005). When exposed to the odor of its pollen host, western skunk cabbage (*Lysichiton americanus*), the stapylinid *Pelicomalius testaceum*, showed an enhanced response to yellow paper targets with a spectral reflectance similar to that of *L. americanum* spathes (Pellmyr and Patt 1986). Alternatively, host chemicals may have induced anemotaxis. This mechanism could explain the nymph's enhanced response to the gray target in the presence of host odor; i.e., they perceived the gray target as a proximate object within the odor plume. However, anemotaxic behavior may not explain the differences in residence and orientation times in the nymphs or the differential behaviors of adults.

Fluctuations in daily and individual response levels to host odor stimuli may have been caused by unknown factors; e.g., meteorological conditions (Fournier et al. 2005). Internal state conditions may have also influenced *H. coagulata* response to different stimuli, because, at times, they seemed to be attracted to visual cues to the extent that a response to chemical stimuli was not evident. In other herbivorous insects, an internal feedback system predicated on physiological state (e.g., hunger, nutrient, or energy levels) can influence responsiveness to inputs from different sensory modalities (Harris and Miller 1988, Bernays 1995, Simpson and Raubenheimer 1996, Behmer et al. 2005, Pompilio et al. 2005).

In this preliminary study, we showed that host odor has a stimulatory effect on *H. coagulata* host-finding behavior and that this insect responds to certain combinations of visual and host odor cues. The nature of the visual and olfactory stimuli that influence *H. coagulata* host-finding behavior, both at proximate and distant scales, still needs to be identified. This will entail examining the main and interactive effects of visual cue components (e.g., reflectance intensity, hue, and chroma) (Todd et al. 1990a, Fukushi 1990, Harris et al. 1993, Bullus-Appleton et al. 2004) and olfactory cue components (e.g., the concentration and composition of volatile compounds in host odors) (Harris et al. 1987, Metcalf and Metcalf 1992, Patt et al. 1995). As well, a determination should be made of the degree to which *H. coagulata* host-finding behavior is influenced by multiple sensory inputs (Prokopy and Owens 1983, Miller and Strickler 1984, Harris and Rose 1990, Harris and Foster 1995, Raguso and Willis 2002, 2004) and internal state condition (e.g., nutritional deprivation level) (Lewis and Takasu 1990, Simpson and Raubenheimer 1996, Behmer et al. 2005, Pompilio et al. 2005). Information generated from these types of

laboratory studies is needed to reveal the behavioral mechanisms underlying the complex landscape-level distribution patterns seen in *H. coagulata.*

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